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Saltmarsh plants, but not fertilizer, facilitate invertebrate recolonization after an oil spill

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Abstract. Foundation species contribute to the recovery of animal communities from disturbance by engineering, by improving habitat quality, and by regulating food availability. In a salt marsh impacted by the *Deepwater Horizon* oil spill, we tested the hypothesis that nutrient subsidies would enhance the positive effects of the foundation species *Spartina alterniflora* on the initial recolonization of benthic invertebrate communities (e.g., copepods, annelids, nematodes) by augmenting food (i.e., microalgae) availability. After two months, plantings of *S. alterniflora* significantly elevated the densities of the polychaete *Capitella capitata*, meiofauna-sized annelids, and total macroinfauna over unplanted plots. After 7 months, the significant effect of plantings persisted for meiofauna-sized annelids, but not for *C. capitata* and total macroinfauna. Plantings had no effect on copepods (including *Nannopus palustris*, the dominant species), nematodes, or microalgal biomass for either month. Nutrient additions did not influence any taxon, despite initial increases in benthic microalgal biomass after 2 months. We hypothesize that the structural effects of plants were important to early colonization, possibly by facilitating larval settlement or ameliorating temperature and desiccation stress. Our results emphasize the importance of re-establishing foundation species in oil-impacted sites to enhance recolonization of saltmarsh annelids, but suggest that recolonization is not promoted by the addition of nutrients.

Key words: benthic invertebrates; chlorophyll *a*; coastal wetlands; *Deepwater Horizon*; oil spill macrofauna; *Capitella capitata*; meiofauna.

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INTRODUCTION

Foundation species such as mangroves, oysters, trees, corals, and grasses define an ecosystem or community by regulating physical structure, abiotic conditions, and trophic interactions (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011). Large-scale disturbances often reduce the abundance of

foundation species, and as a result, ecosystem recovery frequently tracks the recovery of its foundation species (McGlathery et al. 2012, Fleeger et al. 2015, Zengel et al. 2016). As a structuring force for animal communities, foundation species have both trophic and non-trophic roles. Ecologists have long recognized the structural (non-trophic) effects of foundation species on shaping animal

communities by creating or modifying habitat (i.e., ecosystem engineering; Jones et al. 1994) or by ameliorating physical and chemical stress (i.e., facilitation; Bertness and Hacker 1994, Bruno et al. 2003). Recently, ecologists have also highlighted the trophic role of foundation species, which can directly supply food (e.g., direct herbivory on grass) or indirectly control food availability (e.g., via shading; Whitcraft and Levin 2007, Miller et al. 2015, van der Zee et al. 2016).

Resource subsidies can also shape animal communities by enhancing existing energy sources or providing alternative ones (i.e., bottom-up control; Polis et al. 1997). From a restoration perspective, resource subsidies may enhance the recovery of animal communities by establishing or augmenting food availability. For instance, allochthonous input of leaf litter from forests into streams is an important energy subsidy that drives not only total ecosystem production, but also food-web structure, biodiversity patterns, and energy flow (Johnson and Wallace 2005). As a result, restoration of stream communities can track forest restoration (Stone and Wallace 1998). Thus, resource subsidies coupled with the establishment of foundation species should accelerate recolonization by animals after a disturbance. We explore this hypothesis in the early development of a benthic animal community in salt marshes severely damaged by the *Deepwater Horizon* oil spill.

On 20 April 2010, the *Deepwater Horizon* drilling platform exploded and the blowout of the Macondo wellhead released 3.19×10^6 barrels (5.07×10^8 L, judicially decreed) of crude oil into the Gulf of Mexico (U.S. District Court. 2015). Of Gulf Coast wetlands oiled, ~95% were in Louisiana, home to the nation's largest and most productive wetland-estuarine environment. As such, Louisiana's vast coastal wetlands contribute significantly to the \$40 billion annual Gulf economy generated from fisheries and tourism (Deegan 1990, Engle 2011, Oil Spill Commission 2011). Marsh plant and animal mortality were high in the areas that were heavily oiled, leaving behind large areas of marsh denuded of vegetation and bereft of animals (Lin and Mendelssohn 2012, Mendelssohn et al. 2012, Fleeger et al. 2015, Zengel et al. 2016). With billions of dollars devoted to Gulf Coast restoration (NOAA 2016), critical evaluation of potential restoration methods is needed.

Transplantation is a common technique to restore degraded salt marshes (Broome et al. 1988, Lin and Mendelssohn 1998). Saltmarsh plants such as *Spartina alterniflora* are foundation species that regulate marsh structure (Kirwan and Megonigal 2013), ecosystem processes (Baustian et al. 2012), and community structure (Johnson et al. 2007). In terms of structuring communities, marsh plants are strong facilitator species that enhance the survival of co-occurring species by ameliorating physical stress (Bertness and Hacker 1994, Bruno et al. 2003, Whitcraft and Levin 2007; Johnson and Williams 2017). If facilitation is an important process in community regulation, then it may be an important mechanism in promoting animal colonization (Silliman et al. 2015). Saltmarsh plants also directly support herbivores and detritivores through their production of plant material and indirectly by regulating the production of other primary producers such as benthic microalgae (Teal 1962, Thompson 1984, Whitcraft and Levin 2007, Johnson and Jessen 2008).

Although saltmarsh food webs have long been considered detrital-based (Teal 1962), micro- and macroalgae are also important food for many benthic invertebrate species (Haines 1976, Galván et al. 2008, Pascal et al. 2013). In degraded or created marshes, the slow (years-to-decades) development of the detrital pool may be insufficient to meet the energetic needs of primary consumers early in recovery. However, benthic microalgae are a rapidly responding food source. Salt marshes are nitrogen limited, and thus, nitrogen amendments, which promote algal production, may accelerate the early re-establishment of benthic communities when coupled with the structural effects of plantings. Additionally, nitrogen additions may promote the development of an algal-based food web (Levin et al. 2006).

We conducted manipulative experiments of nutrient additions and *S. alterniflora* plantings in a heavily oiled marsh in Louisiana to test the effect of foundation species and a nutrient subsidy on the early development of benthic microalgae and invertebrate communities. We hypothesized that the resource subsidy from fertilization coupled with the plantings of *S. alterniflora* would augment the invertebrate recolonization over the presence of foundation species or fertilization alone.

METHODS

Twenty oil-spill restoration plots (2.1×2.1 m) were established in April 2014 in northern Barataria Bay, Louisiana, along a saltmarsh shoreline (29.44105° N, 89.93337° W) that extends over a linear distance of ~ 100 m (Fig. 1). Based on data from the Shoreline Cleanup Assessment Technique developed in the aftermath of the *Deepwater Horizon* spill, this shoreline was heavily oiled in 2010 (Michel et al. 2013, I. Mendelssohn and Q. Lin, *personal observation*). We picked five locations within this area, separated by 12–30 m, for the experiment. Within each location, we established four 2.1×2.1 m plots in unvegetated areas within ~ 3 m of the shoreline. Each plot within a location was then randomly assigned one of the

following treatments: (1) unmanipulated (no transplants and no fertilizer) to serve as controls, (2) transplants only, (3) fertilizer only, and (4) a combination of transplants and fertilizer. *Spartina alterniflora* plants (hereafter *Spartina*), up to 90 cm tall, were transplanted in designated plots at a density of 3–5 stems/plug, spaced 30 cm apart, and planted 10 cm deep with a total of 64 plugs for each plot. Fertilized plots received slow-release fertilizer (Osmocote Plus; 15% N, 8% P_2O_5 , and 11% K_2O) in April and September 2014 at a rate of $326 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $76 \text{ kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and $198 \text{ kg K}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Fertilizer was inserted 10 cm beneath the soil surface to promote efficiency of nutrient release and to minimize leaching. Fertilizer was added below transplanted *Spartina* roots in plots receiving nutrient

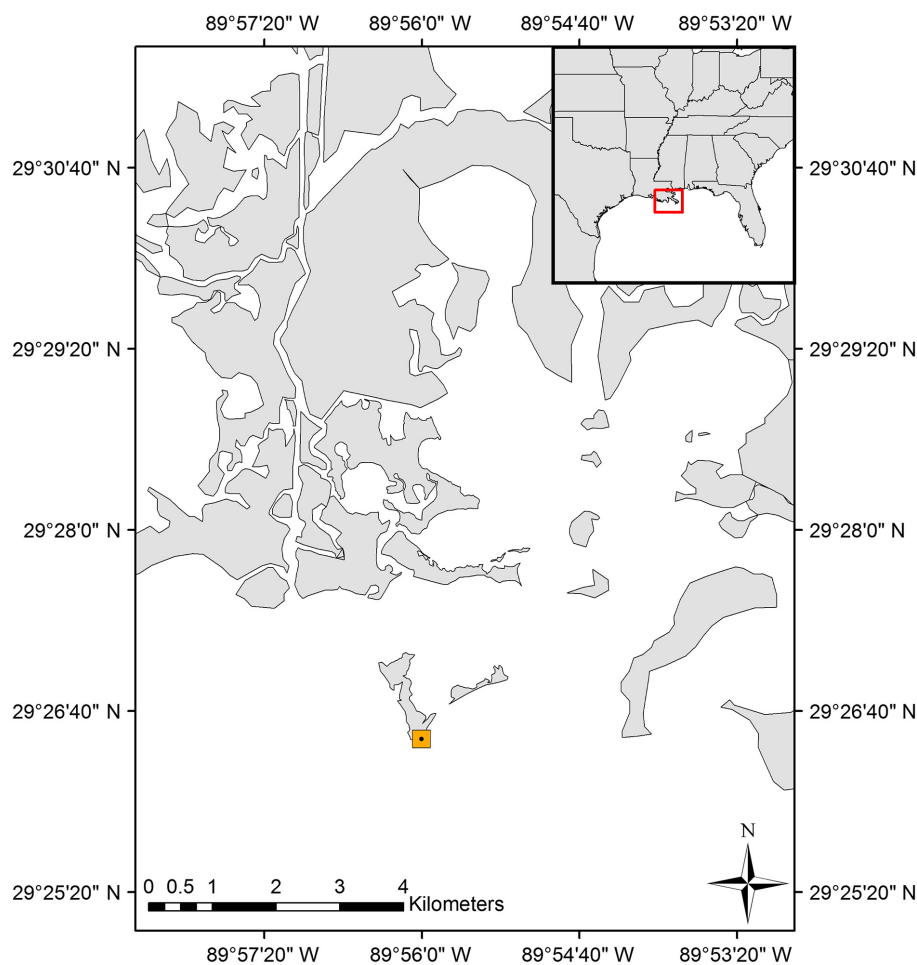


Fig. 1. Location of restoration plots (square) in Barataria Bay, Louisiana.

and *Spartina* amendments. Samples were collected from restoration plots 2 and 7 months (June and November) after initiation.

Biological sampling

Vegetation and benthic samples were taken from a 60 × 60 cm quadrat haphazardly positioned within each 2.1 × 2.1 m plot. The quadrat was placed in a different location on each sampling event to prevent resampling the same location.

Plant biomass and total nitrogen.—Because foundation species are often used as indicators of restoration success, we collected aboveground biomass of our transplant plots by clipping all plants rooted within the sampling quadrat to the ground surface and separated into live and dead components by species. Although we planted only *S. alterniflora*, other species such as *Distichlis spicata* also colonized the plots. The aboveground plant material was dried to a constant mass at 60°C and weighed. We analyzed total nitrogen with elemental analysis from soil collected with a McCalley peat corer (7.6 cm diameter) from each plot.

Soil total petroleum hydrocarbons.—To verify the status of our restoration plots as previously oiled, we determined residual total petroleum hydrocarbons (TPH) in the surface soil (0–7.5 cm) within each plot. Samples were placed in glass jars, stored on ice, and transported to the laboratory in coolers for subsequent analysis. Soil TPH was extracted with dichloromethane and determined gravimetrically to the nearest 0.0001 g (Lin and Mendelsohn 2012). Soil TPH concentration was expressed as mg/g dry soil.

Benthic microalgae.—After vegetation harvest, a hand-held corer (inner diameter = 1.2 cm) was used to take two sediment cores to a depth of 3 mm within the sampling quadrat. The two cores were combined in a single sample container and immediately frozen on dry ice. In the laboratory, samples were stored at –80°C. Photosynthetic pigments were extracted from entire sediment samples with 4 mL of 100% acetone. The sediment–acetone mixture was sonicated for 30 s. The mixture was refrigerated overnight before centrifugation for 10 min. Samples were filtered (0.2 µm) before analysis. High-pressure liquid chromatography was used to examine photosynthetic pigment concentration and composition (Buffan-Dubau and Carman 2000). A Hewlett Packard 1100 liquid chromatograph consisting of

a 100-mL loop autosampler, a quaternary solvent delivery system coupled to a diode array spectrophotometer, and a Hewlett Packard 1046A fluorescent detector were used. Hewlett Packard HPChem-Station software (Agilent, Santa Clara, California, USA) was used for data analysis. Chlorophyll *a* (Chl *a*), expressed as µg Chl *a*/cm², is used here as a proxy for microalgal biomass.

Infauna.—Two additional sediment cores (inner diameter = 3.5 cm) were taken to a depth of 2 cm from the sampling quadrat. Both cores were combined into a single sample cup and fixed in 4% formalin in the field. Cups were shaken to break up soil clumps and to mix with formalin. Formalin was replaced within 24 h when a solution of rose bengal was added. In the laboratory, samples were sieved through a 500-µm sieve stacked on top of a 63-µm sieve. All materials, including roots, rhizomes, and macroinfauna, retained on the sieve were preserved for later analysis. Fauna retained on the 63-µm sieve were extracted from sediments using Ludox. Eighty milliliters of Ludox (Grace, Columbia, Maryland, USA) was added to the sample, which was thoroughly shaken to mix sediment and Ludox. Samples settled for 1–1.5 h before the supernatant was carefully poured through a 63-µm sieve and rinsed. This procedure was repeated twice more.

Meiofauna (metazoans that passed through the 500-µm sieve and collected on the 63-µm sieve) were identified and enumerated to higher taxonomic rank (e.g., nematodes, copepods, polychaetes) using a stereo-dissecting microscope, though the number of the sabellid polychaete *Manayunkia aestuarina* was recorded during rough sorting. Adult copepods were picked from the sample and identified to species. Macroinfauna (invertebrates retained on the 500-µm sieve) were picked from organic matter and identified to the lowest possible taxon.

Statistical analysis

All analyses were conducted in R (R Development Team 2014). To test the effect of fertilization, *S. alterniflora* transplants, and month on microalgal biomass and the abundance of dominant benthic taxa (nematodes, total copepods, the copepod *Nannopus palustris*, meiofauna-sized annelids, the polychaete *Capitella capitata*, and total macroinfauna), data were analyzed with a linear mixed-effect model using the *lme* function in the nlme

package in R (Pinheiro et al. 2015). Our statistical model was a randomized complete block design (different locations as blocks) with *S. alterniflora* plantings, fertilization, and month as fixed effects and blocks (locations) as random effects. All animal data were log ($x + 1$)-transformed prior to analysis to meet assumptions. To generate *P*-values from these models, we used the ANOVA function. When significant interactions were detected, we used the *lsmeans* function from the *lsmeans* package to conduct contrasts within each month (Lenth and Herva 2015).

RESULTS

While *Spartina alterniflora* plantings had a significant effect on the densities of the polychaete, *Capitella capitata* (transplant, $F_{1,25} = 5.25$, $P = 0.03$), the effect was influenced by the month of sampling (transplant \times month interaction, $F_{1,25} = 5.16$, $P = 0.03$). After 2 months, average *C. capitata* densities were significantly higher in planted plots than in unplanted plots (least-square means contrast, $t_{25} = 3.24$, $P = 0.003$); however, that trend disappeared after 7 months (least-square means contrast, $t_{25} = -0.04$, $P = 0.97$; Fig. 2). A similar trend was seen when examining the densities of the total macroinfauna community, in which there was a significant transplant by month interaction ($F_{1,28} = 8.01$, $P = 0.009$; Fig. 2), with significantly higher densities in the planted plots after 2 months vs. unplanted plots (least-square means contrast $t_{28} = 4.99$, $P < 0.0001$), but no differences between planted and unplanted plots after 7 months (least-square means contrast $t_{28} = 0.993$, $P = 0.33$). No main or interactive effect of fertilizer was found for *C. capitata* or total macroinfauna. Because *C. capitata* numerically dominate (63%) the macroinfauna community (Appendix S1: Table S1), the trend in the total macroinfauna community is likely driven by *C. capitata* responses.

In *S. alterniflora* transplant plots, aboveground biomass was significantly impacted by an interaction between month and transplant treatment ($F_{1,28} = 32.64$, $P < 0.0001$). After two months, aboveground biomass was, on average, $34 \times$ higher in planted plots than in unplanted plots (Fig. 2). After seven months, however, the aboveground biomass in unplanted plots increased greatly due to the successful colonization of *Distichlis spicata*, which averaged 63% of the total

aboveground biomass, with *S. alterniflora* comprising the remainder (Q. Lin, *unpublished data*). This resulted in aboveground biomass being $2 \times$ higher in planted vs. unplanted plots. Fertilizer, regardless of *S. alterniflora* transplants, increased aboveground biomass by a factor of $\sim 1.5 \times$ compared to control plots, which was marginally significant ($F_{1,28} = 3.61$, $P = 0.07$; Appendix S1: Tables S2, S3). Mean TPH values ranged from 0.58 to 0.90 mg/g soil in restoration plots after two months (Appendix S1: Table S2).

Spartina alterniflora transplants significantly increased the densities of meiofauna-sized annelids (main effect of transplants, $F_{1,28} = 17.13$, $P < 0.0001$; Fig. 2; Appendix S1: Tables S3, S4), which did not interact with either fertilization or month. There was a significant effect of month on meiofauna-sized annelids ($F_{1,28} = 32.06$, $P < 0.0001$; densities were higher after seven months compared to month 2), which did not interact with either fertilization or transplants. The most commonly observed meiofauna-sized annelids were recently settled juveniles of polychaetes (e.g., *Capitella capitata*) and oligochaetes. No main or interactive effect of fertilizer was found for this taxon. There was a significant effect of month on the copepod *Nannopus palustris* ($F_{1,28} = 5.09$, $P = 0.03$) and nematodes ($F_{1,28} = 23.06$, $P < 0.0001$), in which their densities were higher after two months than after seven months (Fig. 2). There were no effects of transplants or fertilizer on these taxa.

The interaction of fertilizer and month had a significant effect on benthic chlorophyll *a* ($F_{1,28} = 4.02$, $P = 0.05$). After two months, average chlorophyll *a* biomass was significantly higher in fertilized plots than in unfertilized plots (least-square means contrast, $t_{28} = 2.20$, $P = 0.04$); however, that effect disappeared by month 7 (least-square means contrast, $t_{28} = -0.64$, $P = 0.53$; Fig. 2). Neither fertilizer, transplants, nor month affected the densities of total copepods or soil nitrogen (Appendix S1: Table S3; Fig. 2).

DISCUSSION

Within two months, plantings of the foundation species *Spartina alterniflora* in a previously unvegetated, oiled marsh enhanced annelid densities—which were dominated by the polychaete *C. capitata*—over unplanted sites. This effect persisted after seven months for meiofauna-sized

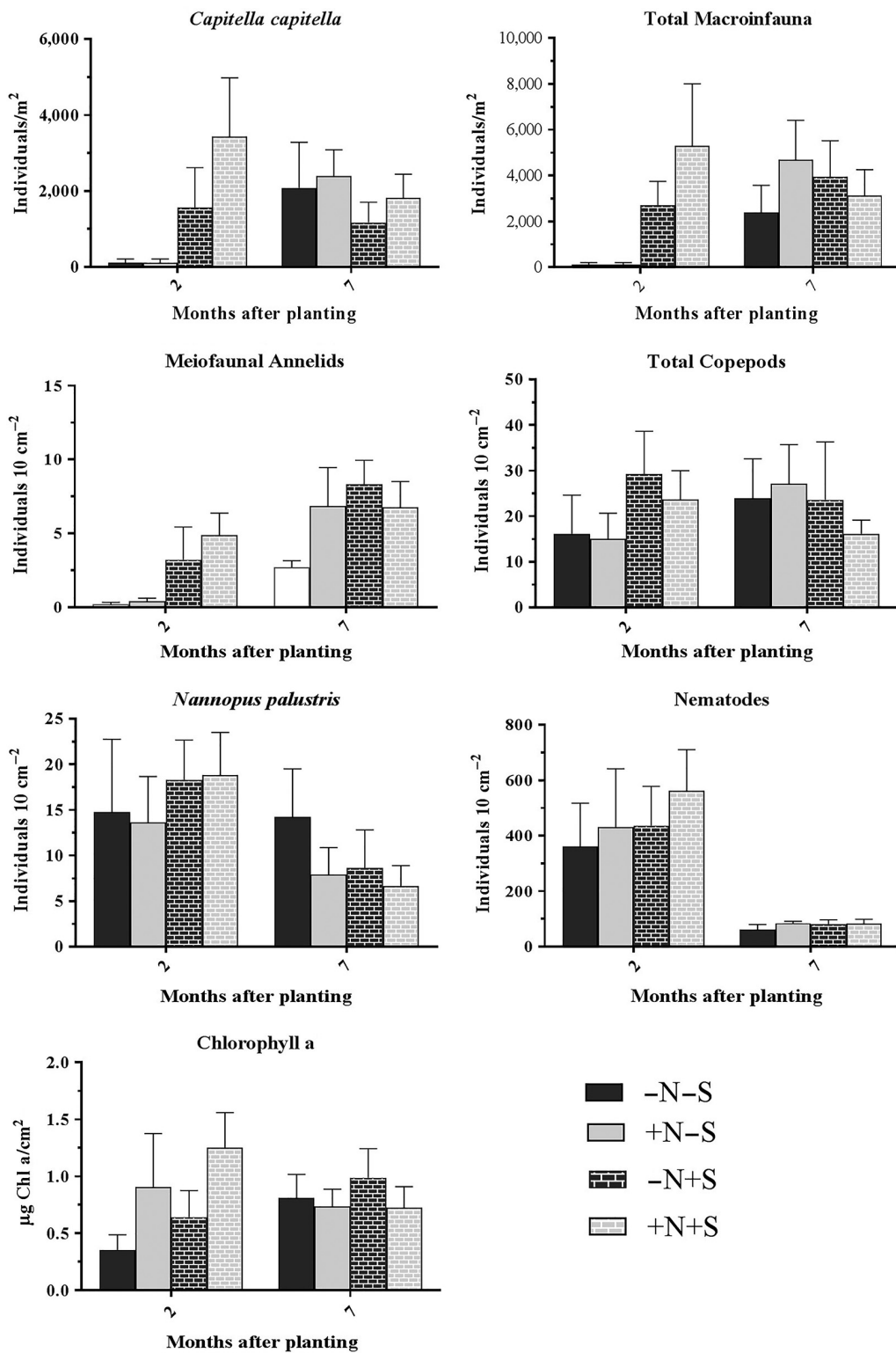


Fig. 2. Mean (± 1 SE, $n = 5$) response of infauna taxa and chlorophyll *a* to restoration treatments. -N = no nutrients added, +N = nutrients added, -S = no *Spartina* transplant, +S = *Spartina* transplant.

annelids (i.e., juvenile *Capitella capitata* and oligochaetes), but not for macrofauna-sized annelids. Fertilizer had no influence on animal densities despite initial increases in benthic microalgal biomass after two months. Our results suggest that re-establishing foundation species is critical to enhancing recolonization of *C. capitata* in the saltmarsh benthos after an ecosystem disturbance. *Capitella capitata* is a frequent and prominent early colonist in soft sediment ecosystems that promotes the breakdown of organic matter. Early colonization by *C. capitata* may therefore contribute to community resiliency as a pioneer species that facilitates later colonists.

After two months, the positive effect of *Spartina* plantings was strongest on both macroinfaunal and meiofaunal annelids, which were dominated by the polychaete *C. capitata*, but had no impact on other invertebrates. Given the large scale of the oiled shoreline, and thus the disturbance (100s of hectares; a type II disturbance; sensu Connell and Keough 1985), these early marsh colonizers likely arrived via the water column. *Capitella capitata* is an opportunistic species with pelagic, free-swimming larvae (though they can have direct-developing larvae in certain instances, Henriksson 1969, Rosenberg 1976) that is commonly one of the first species to colonize disturbed or polluted saltmarsh soils (Sacco et al. 1994, Posey et al. 1997). The presence of vegetation may have facilitated higher densities of *C. capitata* in a number of ways. Plant canopies lower soil temperatures and, in turn, enhance invertebrate densities (Whitcraft and Levin 2007). Laboratory and field studies confirm that the physical presence of stems slows water flow and facilitates settlement (Palmer 1986, Leonard and Croft 2006), which can influence benthic community structure (Neira et al. 2006). By 7 months, the effect of *Spartina* plantings persisted on meiofauna-sized annelids, but not on macrofauna-sized *C. capitata*. The lack of effect of plantings on *C. capitata* may be due, in part, to the colonization of unplanted plots by *Distichlis spicata* and *S. alterniflora*, which caused unplanted plots to resemble planted plots in terms of aboveground biomass.

Although we did not specifically test the structural (slowing water flow) vs. trophic (food) effects of *Spartina* on infauna, we found no difference among treatments for soil organic matter (Q. Lin, unpublished data). This result suggests that

trophic support from *S. alterniflora* was likely equivalent across treatments. Moreover, *S. alterniflora* did not influence microalgal biomass, indicating that the influence of this foundation species on animal communities was due to structural effects (e.g., stress amelioration, facilitating larval settlement) rather than trophic stimulation (Miller et al. 2015, van der Zee et al. 2016).

Fertilizer additions stimulated benthic microalgae within the first two months, but not invertebrate densities. Many benthic invertebrates are generalist feeders (Galván et al. 2011), and this trend may reflect the weak interaction strength between benthic invertebrates and benthic microalgae. The lack of a bottom-up effect of fertilizer on saltmarsh infauna has been seen in other fertilization experiments. For instance, in two separate long-term fertilizer studies in salt marshes, Wiltse et al. (1984) found no effect of fertilizer on infauna density after 5 yr and Johnson and Fleeger (2009) and Mitwally and Fleeger (2013) found limited density responses after 3–6 yr. Mitwally and Fleeger (2014), however, found that although nematode density was unaffected by 6 yr of fertilization, the nematode community was greatly altered.

While we showed that nutrient subsidies had no effect on the early recolonization of saltmarsh invertebrates, other resource subsidies may be important. For instance, Levin and Talley (2002) found that additions of kelp detritus enhanced macroinfauna colonization in a created marsh. Craft and Sacco (2003) estimated that during marsh restoration, 500 g/m² of live belowground biomass is necessary to support infaunal densities of reference marshes. Our sites did not reach this value (Q. Lin, unpublished data), suggesting that poor habitat quality was unable to support the full complement of infauna. Belowground biomass recovers slowly from oil spills (Culbertson et al. 2007, Lin et al. 2016, Fleeger et al. 2017), suggesting that the relative importance of structural vs. trophic effects of foundation species may vary over time. From a restoration perspective, interring detritus into saltmarsh soils at large scales is impractical. From an ecological perspective, we suggest that in the short term, aboveground biomass is important for its structural effects, whereas belowground biomass becomes more important in the long term for its trophic support of infauna.

The densities of most of the infauna were orders of magnitude lower in our treatment plots than those in nearby unoiled sites (D.S. Johnson and J.W. Fleeger, *unpublished data*). Persistent hydrocarbon (e.g., polyaromatic hydrocarbon) contamination associated with marsh soils and/or re-oiling events caused by storms (Rabalais and Turner 2016) may have contributed to the slow recovery, which is common in marsh soils after an oil spill (e.g., Culbertson et al. 2007), although oil toxicity likely declined over time in marsh soils after the *Deepwater Horizon* spill (Duan et al. 2017). In a companion oil-spill recovery study in Louisiana, Fleeger et al. (2017) found that some infaunal taxa did not recover after six years in oiled sediment. However, restoration of the infaunal community in general (e.g., even in the absence of oiling) is slow in salt marshes. For example, after eliminating tidal restrictions and restoring hydrology to salt marshes in Connecticut, Warren et al. (2002) found that it took 20 yr for the epibenthic (amphipods, isopods, snails) community to return to reference levels. Craft and Sacco (2003) found that densities of the polychaete *Manayunkia aestuarina* in created marshes did not achieve equivalence to natural marshes until 8 yr after creation.

CONCLUSIONS

Our results emphasize the importance of re-establishing foundation species to enhance the establishment of some early colonizers, such as *Capitella capitata*, in salt marshes after a disturbance, but suggest that colonization is not enhanced by nutrient subsidies. Nutrient additions have been used in wetland restoration to stimulate aboveground plant growth. Added nutrients, however, can have negative effects on salt marshes by reducing belowground biomass (Darby and Turner 2008, Graham and Mendelsohn 2015) and, in some instances, lead to marsh loss (Deegan et al. 2012). Our work does not justify nutrient subsidies in marsh restoration to stimulate animal communities. Mechanistically, our work indicates that structural effects of plants, specifically aboveground biomass, are more important for initial recovery of marsh animals than plant effects on food supply. In the longer term, however, the trophic role of plants may become more important to the benthic community as animal densities increase and the detrital pools develop.

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